CLASSIFICATION OF THE SPECIES OF THE *HARPALUS* SUBGENUS *GLANODES* CASEY (CARABIDAE: COLEOPTERA)[1]

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Abstract

The subgenus *Glanodes* is represented in the arid grasslands of southwestern United States, including Utah, Arizona, New Mexico, and western Texas by 6 species: *corpulentus* Casey, 1914; *puncticeps* Casey, 1914; *huachuca* NEW SPECIES (type locality: Huachuca Mts., Arizona); *stephani* NEW SPECIES (type locality: Arivaca, Arizona); *obliquus* Horn, 1880; and *cohni* NEW SPECIES (type locality: Marfa, Texas). Listed as a species inquirendum is *Glanodes regressus* Casey, 1914. The new name *Harpalus tadorcus* is proposed for *Harpalus cordatus* LeConte, 1853, a junior homonym of *H. cordatus* Duftschmid, 1812. The subgenus *Glanodes* and its included species are defined and described in terms of adult characteristics. A key is presented to the males of the species. The phylogeny and zoogeography of *Glanodes* is considered in relation to hypothetical transformation series of body structures, and in relation to the history of the arid grasslands in the southwest. It is proposed that the subgenus originated in the late Miocene in the area of the Colorado Plateau and spread south from there, with differentiation taking place when the grasslands contracted under the influence of unfavorable conditions leading to range disjunction of the habitat and of the *Glanodes* populations. Dispersal of the beetles occurred during periods favorable for expansion of the grasslands.

Introduction

The genus *Harpalus* is a large and varied group of mesophilous to xerophilous carabids, ranging in aggregate from southern Africa throughout the whole of the Palaearctic and Nearctic Regions except the arctic tundra. The genus is represented in temperate Mexico, south to the Trans-Volcanic Sierra in the vicinity of Mexico City. Most Nearctic species live in drier areas. On the whole, the taxonomy of North American species of *Harpalus* is not well worked out, although Lindroth (1968) provided a classification based on the Canadian-Alaskan fauna. I am extending Lindroth's study, and this paper deals with a minor but interesting portion of the genus.

In 1914, Casey erected *Glanodes* as a genus separate from, and not closely related to, *Harpalus*. In it he included 4 nominal species, 3 of them proposed as new, all from southwestern United States. One of these is of uncertain status. The others are probably valid species, but Casey did not prove it.

I first became interested in *Glanodes* in 1957 when I was working on another group of harpalines, the genus *Eurycerus* LeConte. To determine the status of *Eurycerus*, I wanted to know something about the other genera which clustered around *Harpalus*. Hence, I examined representa-

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tives of *Glanodes*—in fact, the types of the Casey species. At that time, I concluded 2 things: 1) *Glanodes* should be included in *Harpalus* as a subgenus; 2) *Glanodes* was probably monobasic. The first conclusion was published (Ball 1960a: 62), but the second one was not published.

In 1967, I returned to the study of *Harpalus*, specifically to the fauna of Mexico and southwestern United States, and determined to dispose of the *Glanodes* problem. By this time, I had collected a few specimens of my own on several expeditions to the southwest and also had borrowed types and additional material. Just enough material was available to convince me that my original estimate was in error; the group included more than 1 species, but I could not determine how many nor how they were distributed. So, the problem was left in abeyance. Additional specimens collected in 1967, 1969, and 1971 provided sufficient evidence to enable me to reach the conclusions given in this paper about the definition and classification of members of this subgenus.

Acknowledgements

I am grateful to the individuals and institutions listed in the materials and methods section for the loan of specimens essential to this study. Illustrations were prepared by J. S. Scott, of my Department. A preliminary draft of the manuscript was read and criticized by my colleagues D. R. Whitehead and G. R. Noonan.

Material

This study is based on examination of 137 adult specimens of *Glanodes*, including female specimens which could not be identified and the types of the nominal species. Specimens were borrowed from the following sources (indicated in the text by the abbreviations associated with them):

AMNH—American Museum of Natural History, New York City, N. Y. (Patricia Vaurie)
ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia, Pa. (S. S. Roback)
CAS—California Academy of Sciences, San Francisco, California (Hugh B. Leech)
FMNH—Field Museum of Natural History, Chicago, Illinois (R. L. Wenzel)
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (P. J. Darlington, Jr.)
NMNH—National Museum of Natural History, Washington, D. C. (R. Gordon)
OSUC—Ohio State University, Columbus, Ohio (C. A. Triplehorn)
TLE—Terry L. Erwin collection, National Museum of Natural History, Washington, D. C.
TTUL—Texas Technical University, Lubbock, Texas (C. W. O'Brien)
UASM—Strickland Museum, University of Alberta, Edmonton, Alberta, Canada
UCB—University of California, Berkeley, California (J. Chemsak)

UKL—Snow Entomological Museum, University of Kansas, Lawrence, Kansas (G. W. Byers)
KSC—Karl Stephan, 3038 E. Eastland, Tucson, Arizona

Methods

Descriptions: Because members of this subgenus are all similar in external characteristics, species descriptions are brief. Characters common to all species are included in the description of the subgenus.

Analysis of variation: This was done for body length and for character of discriminatory value. Numerical data are presented in Tables 1 to 4. Standard statistics were computed for length and for 3 ratios, for those samples including 9 or more individuals. For samples of more than 1 but less than 9, only means were computed. Comparisons were made among larger samples by t- tests of mean differences. Some numerical data are presented in Graph 1.

Measurements: The following measurements were made with an ocular micrometer in a stereoscopic binocular microscope. The length represented by a micrometer scale interval at a magnification of 40X was 0.04mm.

Head length: straight-line distance from base of mandible to posterior margin of compound eye, on left side of head.

Pronotum length (PL): straight-line distance from apical to basal margin, measured along mid-line.

Elytra length (EL): straight-line distance from basal carina to apex of longer elytron.

"Standardized body length": sum of measurements described above. In my previous publications, I used the term "total length" for this sum, and hoped that other students of carabids would adopt this usage. This has not happened, and total length means different measurements to different workers. Therefore, I abandon the term "total length" for descriptive purposes and use the above designation in its place.

The following measurements (used to form ratios, as indicated in the text) of male genitalia parts are indicated on Fig. 4a and 4b: *Length of median lobe* (G: ML): straight-line distance from base to apex. *Length of apical portion of shaft* (G:MLAP): straight-line distance on dorsal surface from apex of membranous area to apex of median lobe. *Width of apex of median lobe* (G: MWA): straight-line distance across apex, measured on ventral aspect. *Length of macrospine V of internal sac* (G: ILV): straight-line distance from base to apex of macrospine V.

Illustrations: Line drawings were prepared with the aid of a camera lucida mounted on a Wild M5 stereoscopic microscope.

Recognition, grouping, and ranking: The identity of specimens was determined in part by study of the literature and in part by comparison with type specimens. The types of 3 nominal species are females which lack most or all distinctive characteristics of their respective species. Two were associated with their respective species by coincidence of geographical ranges. One type could not be so associated because its locality of collection is adjacent to the ranges of 3 species, and its name is assigned to the category "species inquirendum".

The categories used are species and subgenus. Because few specimens

are available, it is impossible to be sure that character differences indicate real species differences. Of 6 species recognized, 3 have ranges which evidently partially overlap and are judged to be sympatric (Fig. 13). Males assigned to these species differ in details of the genitalia: form of apical portion of median lobe and proportions of larger spine of internal sac. It is assumed that discontinuities of this magnitude would not be observed among sympatric groups of males unless they represented reproductively isolated populations—hence different species. Allopatric males were judged conspecific if they exhibited substantial identity in genitalic characteristics. They were judged to be specifically different if they differed from one another as much as did the males of different sympatric species. This matter is discussed at greater length below. The decision to rank this complex of species as a subgenus is discussed below.

Structure of the Male Genitalia

Variation in the male genitalia cannot be accounted for in terms of differential growth related to body size (allometry) nor in terms of marked phenotypic variability. The first point was tested by plotting values for various ratios against body size; no correlations were discovered. The second point is best illustrated by noting the general similarity exhibited by the genitalia among groups of *H. obliquus* specimens from different areas (see Graph 1). If the genitalia were simply phenotypically highly plastic, one would expect marked differences between samples from geographically widely separated localities.

The median lobe: This is, in general, average for *Harpalus* specimens; it is an asymmetrical tube, sclerotized all around basally for about half its length, and throughout its length ventrally and on the right side; the membranous area is on the left side (Fig. 4a). The apical portion of the shaft (G: MLAP) is smooth or bears dorsally a series of short projections, called here spinules. The shaft terminates in a more or less expanded apical disc which projects ventrally as a short lip, and more or less dorsally as a pair of spinules referred to here as the discal spinules.

The parameres are typical of *Harpalus* members and do not offer characteristics of taxonomic value.

Structure and vestiture of the internal sac: The internal sacs of *Harpalus* males offer excellent characteristics for identification and classification of species, as shown by Lindroth (1968) for northern North American species, and as shown by Ball and Anderson (1962) for North American species of the subgenus *Pseudophonus*. However, a detailed system of homology and nomenclature of the various structures for the entire genus has not been proposed. I have prepared such a system, and it will be published in the near future. This system is used here to designate the parts of the internal sac of *Glanodes* males.

The following description should be studied in conjunction with Fig. 4 to 11. The aspects of the internal sacs illustrated are lateral, left or right, with the apex of the median lobe directed toward the upper margin of the page. Surfaces are designated as follows. The dorsal side is toward the bottom of the page, ventral toward the top. Sides are designated according to the position of the everted median lobe relative to the long axis of a beetle; the left side of the internal sac corresponds to the

left side of the median lobe when the latter is everted. The basal area of the internal sac is near its point of attachment to the median lobe, the medial area is toward the middle, and the preapical area is toward the distal end of the everted sac.

Briefly, the internal sac of a *Glanodes* male exhibits the following features: a large lobe on the left side (not evident in the illustrations); 2 large spines, named macrospines, and designated by roman numerals (IV, on right side basally, and V, approximately medio-dorsal); 1 to 3 patches of somewhat enlarged scales, named macrotrichia and designated by capital letters (C basal ventral; F, medial left; H, medial right (Fig. 11c)). Macrotrichial fields C and F exhibit variation in number of macrotrichia, and are absent from the internal sacs of some specimens.

Species Discrimination

As indicated above, the major evidence for recognition of *Glanodes* species is the pattern of geographical variation of the male genitalia. The following discussion is based on data presented in Graph 1. This is a scatter diagram, with values for the ratio G: ILV/ML plotted against values for the ratio G: MWA/MLAP, for each individual measured. The lines around groups of specimens do not imply boundaries, but facilitate recognition of the major groups.

The variation pattern is not the simple one which might be expected if there were gene flow among adjacent population samples. Note these 5 points:

1) The groups with the highest values for the ratio G: ILV/ML are *H. cohni* and *H. puncticeps.* The former group is known only from western Texas (Fig. 13), the latter only from northwestern Arizona, and between them are the ranges of *H. obliquus* and *H. stephani.*

2) The groups with the lowest values for this ratio are *H. huachuca* and *H. corpulentus,* with the former occurring in southern Arizona, the latter in Utah, and with the ranges of *H. puncticeps, H. stephani* and *H. obliquus* in between.

3) The ranges of *H. huachuca* and *H. obliquus* overlap in the Huachuca Mountains, but the 2 groups are widely separated, mainly by differences in the values for the ratio G: MWA/MLAP.

4) The Arivaca specimen of *stephani* (coordinates G: ILV/ML-0.25, and G: MWA/MLAP-0.44) approaches the *H. huachuca* specimen very little more than does one of the Baboquivari specimens (coordinates 0.27 and 0.47), although Arivaca is geographically closer to the Huachuca Mountains than are the Baboquivari Mountains. If there were gene flow among these groups, one would expect the Arivaca specimen to occupy an intermediate position between the other 2 groups.

5) The geographical range of *H. cohni* and *H. stephani* approach one another, but the Texas specimen of the latter species (labelled "T" in Graph 1) shows no tendency to be *cohni*-like.

In summary, the data indicate that the variation pattern of these characteristics is not closely correlated with geography. The geographical proximity of 3 of these groups, without clear indication of intermediacy in genitalic characteristics, suggests that genetic interaction is not taking place among the groups. A conclusion seems clearly indicated:

the differences in genitalia are evidence that the different groups are specifically distinct. This conclusion is borne out by additional features of the genitalia as well as by a few external structural characteristics.

Ranking and Relationships of *Glanodes*

The evidence that *Glanodes* is monophyletic, and thus a natural group, is a unique combination of characteristics shared by its members. These characteristics are detailed in the section entitled "diagnostic characteristics". It is not possible at this time to show by phylogenetic interpretation of the data that *Glanodes* should be included in *Harpalus*, but on the basis of phenetic considerations it clearly belongs therein. Although the combination of characteristics is unique, each characteristic itself is within the range of variation of *Harpalus sensu latiore.*

To more closely approximate the numerous important phylogenetic branchings within a genus with the diversity of *Harpalus*, I think it essential to have several infrageneric ranks. For instance, I use the formal category subgenus and semi-formal "group" and "subgroup". My notion of "subgenus" as a taxon is of a group generally equivalent to, or rarely more inclusive than, Lindroth's (1968) "group". The *Glanodes* taxa are not sufficiently different among themselves to warrant introduction of semi-formal categories, although it is necessary to have them for other subgenera of *Harpalus.*

Relationships at the subgeneric level are not clear at present. Members of this subgenus superficially resemble those of *Opadius*, but the internal sacs of the latter are characterized as follows: ventral lobe with spine patch; with macrospines I and VIII. Thus, there is no detailed similarity between *Opadius* and *Glanodes* internal sacs. An enlarged ventral lobe with spine patches seems to characterize the more highly evolved subgenera of *Harpalus*, and I think it is possible that *Glanodes* shared a common ancestry with the ancestors of the former complex.

Graph 1: Diagram illustrating correlation of values for ratios G: ILV/ML and G: MWA/MLAP, for *Glanodes* specimens.

Classification

Subgenus *Glanodes* Casey

Glanodes Casey, 1914: 60. TYPE SPECIES: *Harpalus obliquus* Horn (type by original designation).
Harpalus (*Glanodes*) Csiki, 1932: 1185; Ball, 1960a: 62, and 1960b: 140; Lindroth, 1968: 809.

Diagnostic characteristics: Members of this subgenus most closely resemble those of *Harpalus* (*Opadius*) *tadorcus* NEW NAME[1], but differences in form of the pronotum distinguish the 2 groups readily: *Glanodes* specimens with sides oblique posteriorly, not sinuate; *Opadius* specimens with sides sinuate posteriorly. Lindroth (1968: 809) wrote that these 2 groups were closely related because, in addition to other shared characteristics, the males of each have 2 spines in the internal sac of the genitalia. However, study of the everted internal sac shows that the spines are probably not homologous because they are not in the same relative positions in the members of the 2 taxa.

Head with dorsum punctate between and behind eyes. Elytra posteriorly with ocellate punctures in intervals 5 and 7, and in interval 3 of most specimens; each with single discal seta in or near stria 2. Abdominal sterna 3 to 5 with accessory setae. Tarsal articles with dorsal surfaces glabrous. Mentum edentate. Pronotum with hind angles obtuse, subangulate or broadly rounded; posterior lateral impressions finely punctate. Metepisterna short. Elytra with apices average, not markedly sinuate. Hind wings short stubs. Male genitalia with median lobe average in form and proportions. Internal sac with large left lobe. Macrospines IV and V present, V very large; no spine patches; macrotrichial field H present, fields C and F present or absent (Fig. 4a, 5a, 7a,b, 8, 9a, 11a,c). Sclerites of ovipositor average.

Description: Size average for *Harpalus*, standardized body length of males within 6.5 to 10.5 mm (details in Table 1); females approximately same size.

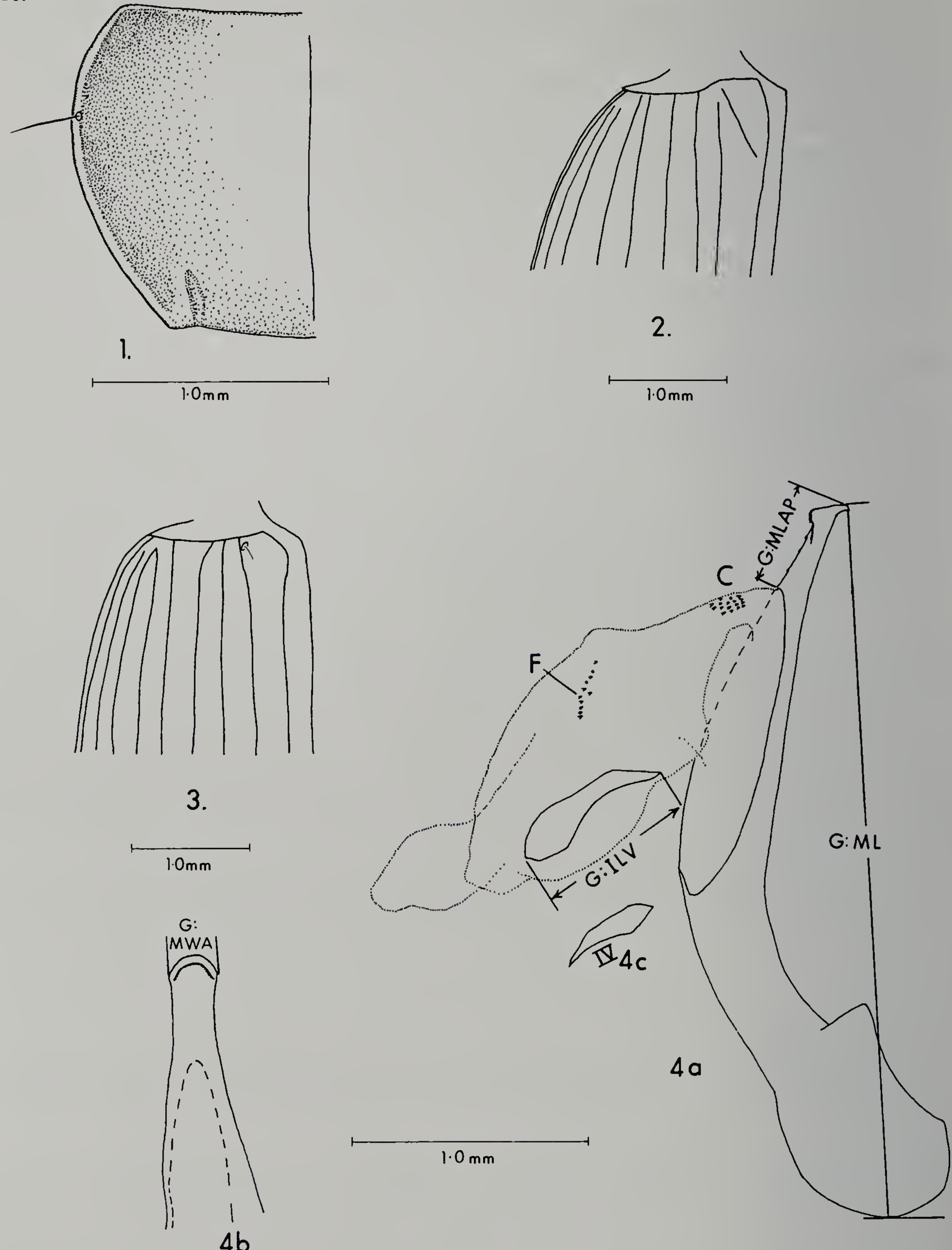
Form: subpedunculate; proportions average (Fig. 12), but body more terete than average.

Color: Body with dorsum rufo—piceous to piceous, almost black in some specimens; venter rufous to rufo- piceous. Antennae, palpi, and legs rufous.

Microsculpture: Labrum, meshes isodiametric, lines distinct. Clypeus and dorsum of head of female with meshes small, isodiametric, lines fine; male, with lines almost effaced, meshes small, isodiametric or slightly stretched; ventral surface of head with lines more or less effaced medially, distinct laterally, meshes isodiametric. Pronotum of females with lines fine, meshes small, stretched, except isodiametric near and in posterior-lateral impressions; among males, meshes indistinct to effaced, generally effaced medially. Proepisterna with meshes stretched longitudinally, lines distinct; Prosternum with lines fine, meshes stretched transversely.

[1]Proposed for *Harpalus cordatus* LeConte, 1853, junior secondary homonym of *Harpalus* (*Ophonus*) *cordatus* Duftschmid, 1812. The specific epithet *tadorcus* is an anagram based on *cordatus*.

Metepisterna and lateral areas of metasternum with lines distinct, meshes slightly stretched; middle of metasternum smooth. Elytra with meshes isodiametric, lines distinct; or meshes stretched, lines very shallow to absent.



1) Pronotum, left half, of *Harpalus stephani*, new species (Baboquivari Mountains, Arizona). 2) Left elytron, basal portion, of *Harpalus puncticeps* Casey (Peach Springs, Arizona). 3) Left elytron, basal portion, of *Harpalus obliquus* Horn (Fort Bayard, New Mexico). 4) Male genitalia of *Harpalus corpulentus* Casey (Wasatch, Utah): a, median lobe and everted internal sac, left lateral aspect; b, median lobe, apical portion of shaft, ventral aspect; c, macrospine IV. Lettering: C and F, macrotrichial fields of internal sac; IV and V, macrospines of internal sac; G: ML- length of median lobe; G: MLAP-length of apical portion of shaft of median lobe; G: ILV- length of macrospine V; G: MWA- width of apex of median lobe, in ventral aspect.

Luster: Dull to shining; ventral surface among most specimens more shining than dorsal surface; no parts of body iridescent.

Macrosculpture: Dorsum of head with coarse punctures, more or less

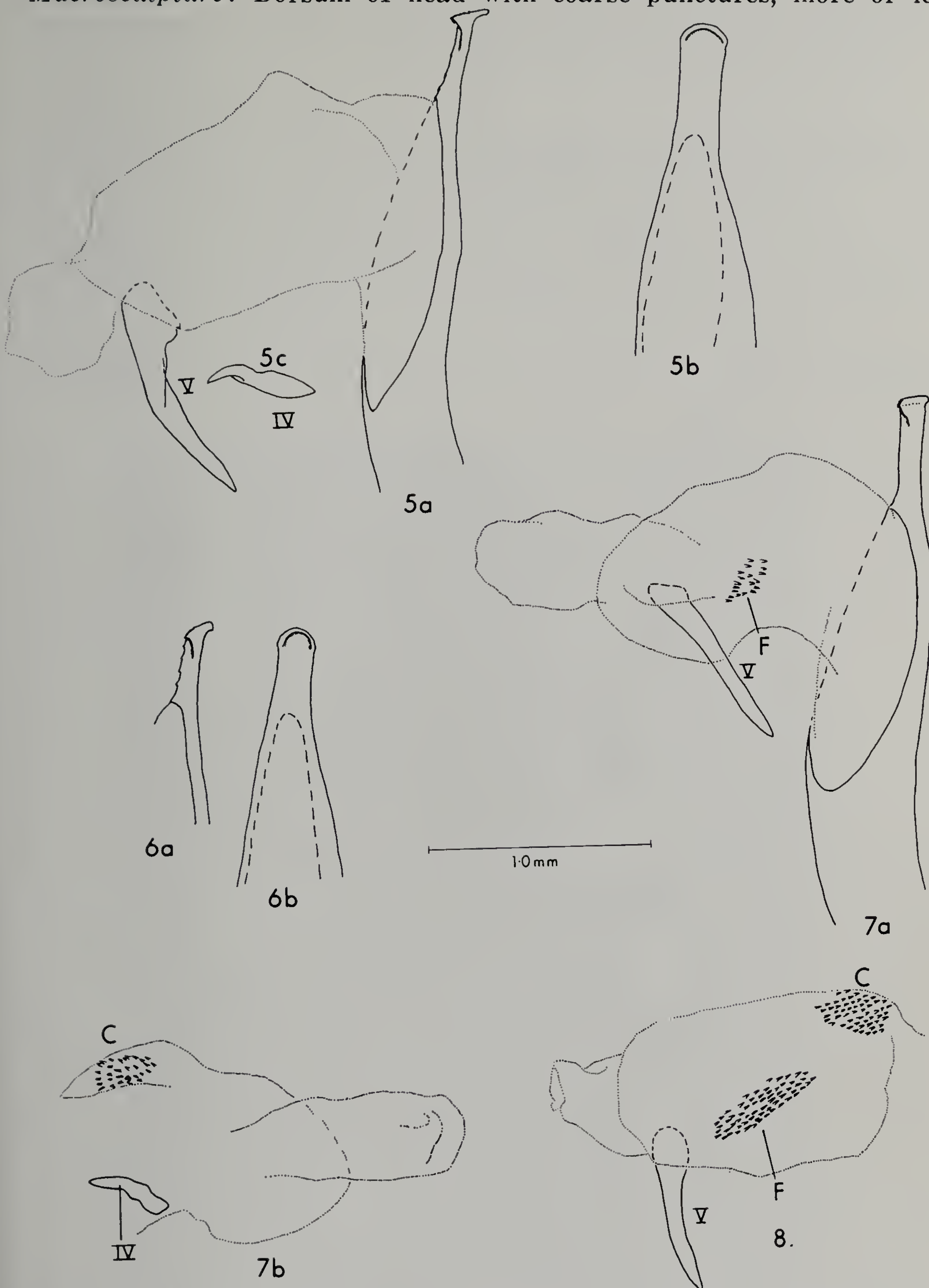


Fig. 5-8. Male genitalia of: 5) *Harpalus puncticeps* Casey (Peach Springs, Arizona) : a, b, c and lettering as in Fig. 4; 6) *Harpalus huachuca*, new species (Huachuca Mountains, Arizona) : a, median lobe, apical portion of shaft, left lateral aspect; b, median lobe, apical portion of shaft, ventral aspect; 7) *Harpalus stephani*, new species (Baboquivari Mountains, Arizona) : a, median lobe, apical portion of shaft and everted internal sac, left lateral aspect; b, internal sac, right lateral aspect. Lettering as in Fig. 4; 8) internal sac, left lateral aspect, of *Harpalus stephani*, new species (Culberson County, Texas). Lettering as in Fig. 4.

deeply impressed. Pronotum with posterior lateral impressions and lateral grooves sparsely, finely punctate.

Vestiture: Submentum with 2 pairs setae, mentum with 1 pair setae. Prosternum with numerous short, fine setae on basal portion; apex of in-

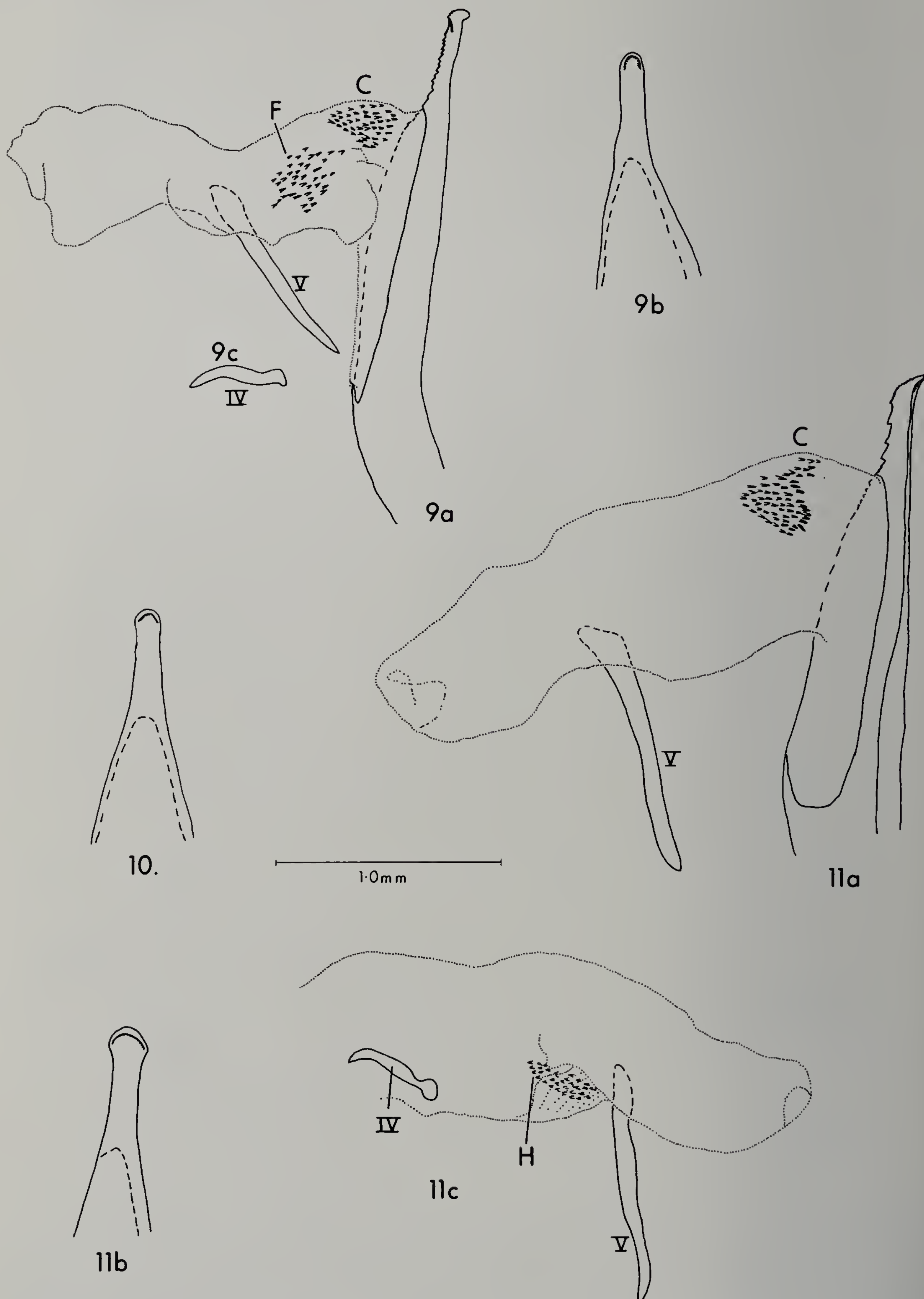


Fig. 9-11 Male genitalia of: 9) *Harpalus obliquus* Horn (Huachuca Mountains, Arizona): a, b, c and lettering as in Fig. 4; 10) median lobe, apical portion of shaft, ventral aspect, of *Harpalus obliquus* Horn (41 mi. sw. Magdalena, New Mexico); 11) of *Harpalus cohni*, new species (Davis Mountains, Texas): a and b as in Fig. 4; c, internal sac, everted, other lettering as in Fig. 4.

tercoxal process with row of setae. Metasternum with row of setae. Middle coxae setose; hind coxae each with 4 to 6 setae; each femur with several rows of long setae. Each elytron with basal area with short fine setae, each side of scutellum; basal puncture; single discal puncture on or near stria 2; intervals 3, 5, and 7 with several setigerous punctures in apical 1/5. Abdominal sterna 3, 4, and 5 with accessory setae; sternum 6 with 4 long terminal setae.

Head: Average for *Harpalus*. Frontal impressions broad, irregular depressions. Antennae extended posteriorly to base of pronotum; scape slightly swollen near base.

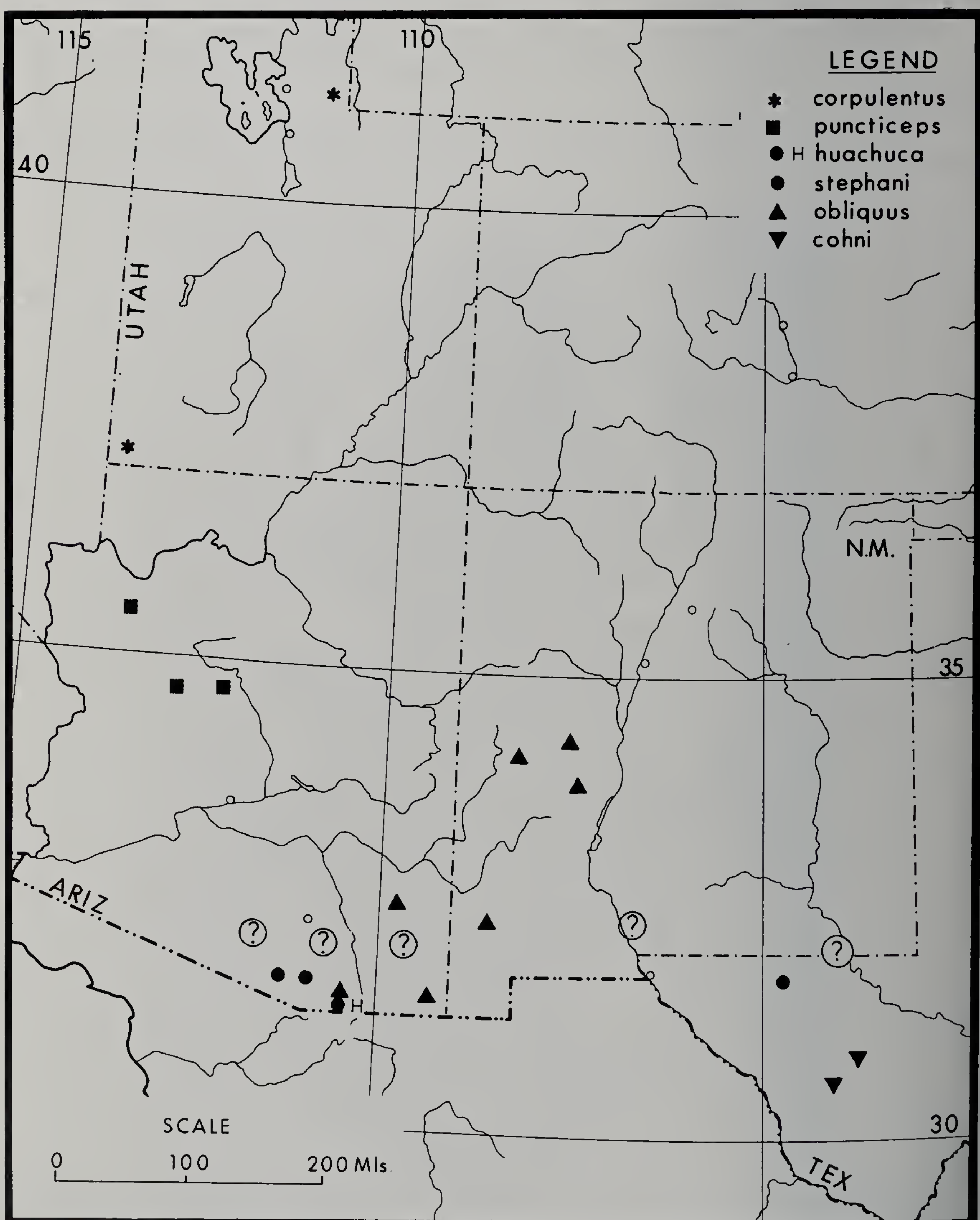
Mouthparts: Labrum, mandibles, and maxillae average. Labium with paraglossae slightly longer than, and adnate almost to apex of, ligular sclerite.

Prothorax: Pronotum (Fig. 1) markedly convex, cordiform; anterior margin almost straight; posterior margin straight or slightly bisinuate

12. Photograph of dorsal surface of male *Harpalus obliquus* Horn (41 mi. sw. Magdalena, New Mexico).

laterally; sides rounded, more strongly constricted posteriorly than anteriorly. Anterior lateral angles rounded, hardly projected; posterior lateal angles rounded, projected slightly posteriorly. Transverse impressions absent; median longitudinal impression shallow; lateral grooves moderately wide, sides more or less distinctly beaded; posterior lateral impressions moderately elongate, shallow. Prosternum with apex of intercoxal process beaded or not.

Pterothorax: Metasternum reduced. Metepisternum as long as wide, about twice as long as metepimeron.



13. Map of southwestern United States, showing distribution of the species of subgenus *Glanodes*. Question marks indicate localities at which unidentified females were collected.

Elytra: Widened gradually to apical 2/5, evenly tapered or slightly sinuate subapically; humeri rounded or angulate. Striae well developed, shallowly punctate; intervals moderately convex.

Hind wings: Short stubs.

Legs: Average for *Harpalus* members, except as noted in diagnosis. Front and middle tarsi of males with articles 1 to 4 with adhesive hairs on ventral surfaces.

Male genitalia: Median lobe average in form and proportions. Internal sac as described in diagnosis, and as figured (Fig. 4 to 11).

Female genitalia and *ovipositor*: Average for members of Harpali.

Geographical distribution: The subgenus *Glanodes* is known from southwestern United States, ranging from the Mexican border northward to northern Utah, and from western Texas to northwestern Arizona. The species are evidently confined to grassland and desert grassland habitats.

Key to Males of the Species of the Subgenus *Glanodes*

1. Elytron with well developed humeral tooth .... 2.

1′. Elytron without humeral tooth, humerus rounded (Fig. 3 and 12) .... 3.

2(1). Male genitalia with macrospine V of internal sac shorter (Fig. 4a); with macrotrichial field C; specimen from locality north of Grand Canyon, in Arizona or Utah .... *corpulentus* Casey, p. 189.

2′. Macrospine V longer (Fig. 5a); without macrotrichial field C; specimen from locality south of Grand Canyon .... *puncticeps* Casey, p. 190.

3(1). Elytral intervals smooth, lines of microsculpture absent or confined to edges of striae; median lobe of genitalia with broad apex (Fig. 11b); specimen from western Texas locality .... *cohni* new species, p. 193.

3′. Elytra with microsculpture lines evident on elytral intervals, meshes isodiametric or transversely stretched .... 4.

4(3). Median lobe with apex narrow in ventral aspect (Fig. 9b and 10) .... *obliquus* Horn, p. 192.

4′. Median lobe with broader apex (Fig. 5b and 6b) .... 5.

5(4). Median lobe with apical portion of shaft smooth dorsally (Fig. 7a); apex viewed in lateral aspect about truncate .... *stephani* new species, p. 192.

5′. Median lobe with apical portion of shaft with spinules dorsally (Fig. 5a and 6a) .... 6.

6(5). Internal sac with macrospine V long (Fig. 5a) .... *puncticeps* Casey, p. 190.

6′. Internal sac with macrospine V short (Fig. 4a) .... *huachuca* new species, p. 191.

Harpalus (*Glanodes*) *corpulentus* Casey

Glanodes corpulentus Casey, 1914: 62. HOLOTYPE female, labelled as follows: "Virg. R. Ut; Casey bequest 1925; TYPE USNM 47736 [red paper]. TYPE LOCALITY—St. George, Utah (here restricted) (NMNH).

Note on type locality: The restriction of the type locality is made to provide a specific place. The restriction is based on study of specimens

compared with the type, each bearing a "St. George" locality label, with style of printing similar to that of the locality label of the type specimen. Indeed, I suspect that the type specimen was probably collected at St. George.

Comparisons: In external features, specimens of this species are most like those of *H. puncticeps*. However, the median lobe of *H. corpulentus* is shorter, with shorter apical portion of the shaft and narrower apex, and with macrospine V of the internal sac shorter (Tables 3 and 4, Fig. 4 and 5). In proportions of the genitalia, males of this species are most like those of *H. huachuca*, but the median lobe of the latter is shorter with shorter apical portion and with shorter macrospine V. Further, the known ranges of these taxa are widely separated (Tables 3 and 4, Fig. 4, 6, and 12).

Description: Data on variation in standardized body length, and in the ratios PL/EL, G: MWA/MLAP and G: ILV/ML are presented in Tables 1 to 4. Variation in the last 2 ratios is correlated in Graph 1. Elytra of males with well developed microsculpture lines, meshes small, isodiametric or slightly stretched; humeri narrowly rounded, each with well developed tooth (cf. Fig. 2), latter smaller than in *puncticeps* males. Median lobe shorter than average, apical portion of shaft short (G: MLAP), dorsally with short spinules; disc well developed, apex oblique, discal spinules well developed (Fig. 4a); apical disc broad (Fig. 4b). Internal sac with microspine V short (Fig. 4a) (G: MWA); macrotrichial field C small, field F very small (Fig. 4a); 3 males dissected.

Geographical distribution: known only from Utah (Fig. 13).

Material examined: 8 specimens from UTAH: Summit County, Wasatch (OSUC); Washington County, St. George (AMNH), Virgin River (MCZ). "Utah". (NMNH).

Harpalus (*Glanodes*) *puncticeps* Casey

Glanodes puncticeps Casey, 1914: 61. HOLOTYPE female, labelled as follows: "Peach Sp'g Arizona Wickham; 1 1 23; Casey bequest 1925; TYPE USNM 47735 [red paper]. (NMNH) TYPE LOCALITY—Peach Springs, Mohave County, Arizona.

Comparisons: Specimens of this species are most like those of *H. corpulentus* in external characters (for details, see discussion of the characteristics of the latter species above). In genitalic characteristics, males of *H. puncticeps* have a long macrospine V, like males of *H. cohni*, and a moderately long apical portion of the shaft as in *H. stephani* males. However, the combination of ratios G: MWA/MLAP and G: ILV/ML distinguish them (Graph 1 and Tables 3 and 4).

Description: Data on variation in standardized body length, and in the ratios PL/El, G: MWA/MLAP, and G: ILV/ML are presented in Tables 1 to 4. Variation in the last 2 ratios is correlated in Graph 1. Elytra of males with well developed microsculpture lines, meshes isodiametric or slightly stretched; humeri of most males each with well developed tooth (Fig. 2), of most females not toothed (Fig. 3). Median lobe longer than average, apical portion of shaft of average length with small spinules throughout length dorsally; apical disc well developed, with well developed discal spinules (Fig. 5a), broad in ventral aspect (Fig. 5b). Internal sac with macrospine V longer than average; macrotrichial fields C and F

various: both lacking (11 specimens), C very small, F lacking (2 specimens), or both small (1 specimen). I dissected 15 males.

Notes on habitat: Specimens were collected on 10-VIII-71, 19 miles south of Frazier's Well, Hualapai Indian Reservation, Arizona, in grassland areas, mainly on flood-plains. Vegetation consisted of grasses, cacti, and small piñon oaks (mainly on the edges of small arroyos). The ground was clay with gravel mixed in, and with stones on the surface. The ground was damp and a nearby arroyo had recently been full of water. The beetles were under dry cattle and horse droppings, under stones, and in piles of plant debris concentrated in lumps by the action of flood water. Other carabids collected in the same area represented the following genera: *Pterostichus* (subgenus *Poecilus*), *Agonum*, *Piosoma*, *Harpalus*, *Selenophorus*, *Discoderus*, and *Bradycellus*.

Specimens of *Harpalus puncticeps* were also collected near Paulden, Arizona on a slope near a small creek, following a very heavy rain. The vegetation was very sparse, including grasses and cacti. The beetles were under dry cattle and horse droppings. Other genera represented were those listed above minus *Bradycellus* and including *Calosoma* and *Stenolophus* (*conjunctus* group). All specimens for which data are available were collected in August, at elevations greater than 5000′ above sea level.

Geographical distribution: known only from grassland areas in northwestern Arizona (Fig. 13).

Material examined: I examined 40 specimens from the following localities in ARIZONA: Coconino County, 19 mi. s. Frazier's Well, about 7 mi. e. Peach Springs, 5300-5400′ (UASM); Mohave County, Peach Springs (NMNH); Hualapai Indian Reservation, Buck and Doe Road, 12.2 mi. n. jct. with U.S. 66, 2.6 mi. e. Peach Springs, 11-VIII-71, 5100′ (UASM); Yavapai County, Grasshopper Flat (UAT); 1.3 mi. s. Paulden, on U.S. 89 (UASM).

Harpalus (*Glanodes*) *huachuca* Ball, NEW SPECIES

Comparisons: In external characteristics males of this species are indistinguishable from males of *H. stephani*. However the 2 groups of specimens are distinguished by differences in the male genitalia (Fig. 6, cf. Fig. 7). The median lobe of the *H. huachuca* male is much shorter, with shorter apical portion of shaft, narrower apical disc, shorter macrospine V of the internal sac and with smaller macrotrichial field C (Tables 3 and 4 and Graph 1).

Description: Values for the following measurements and ratios are presented in Tables 1 to 4: standardized body length, PL/EL, G: MWA/MLAP and G: ILV/ML. Variation in the last 2 ratios is correlated in Graph 1. Elytra of male with well developed microsculpture, meshes isodiametric or slightly stretched; humeri not toothed (cf. Fig. 3). Median lobe shorter than average, apical portion of shaft short with short spinules dorsally throughout length; apical disc oblique, large, discal spinules prominent (Fig. 6a), broad in ventral aspect (Fig. 6b). Internal sac with macrospine V shorter than average, macrotrichial field C very small, field F small.

Type material: HOLOTYPE male, labelled "Huachuca Mts., Ariz. VIII. 10" [handwritten]; (NMNH). The type locality should be more restricted

than the mountain range listed above, but this cannot be done until additional material is found in the vicinity of the Huachuca Mountains. No biological data are available.

Derivation of the specific epithet: the name of the type area, treated as a noun in apposition.

Geographical relationships: The known range is partially within the known range of *H. obliquus*, and probably within the range of *H. stephani* (Fig. 13).

Harpalus (*Glanodes*) *stephani* Ball, New Species

Comparisons: The absence of spinules from the apical portion of the shaft of the median lobe distinguishes the males of this species from all others of *Glanodes*.

Description: Values for the following measurements and ratios are presented in Table 1 to 4: standardized body length; PL/EL; G: MWA/MLAP and G: ILV/ML. Variation in the last 2 ratios is correlated in Graph 1. Pronotum in form as in Fig. 1.

Elytra of males with microsculpture lines well developed, meshes isodiametric or slightly stretched; humeri not toothed. Median lobe straighter than average, apical portion of average length, without spinules dorsally; apical disc well developed, subtruncate apically, with well developed discal spinules (Fig. 7a). Internal sac with macrospine V short, macrotrichial field C large, field F large (Fig. 8) or small (Baboquivari Mts. specimen Fig. 7a).

Type material: Holotype male, labelled: "Arizona Pima County, Arivaca, 8 Sept. 1970, K. Stephan coll." (NMNH). Paratypes: 3 males, Baboquivari Mts., 24-VII-41, R. H. Beamer (UKL); same. E. L. Todd (UKL); Culberson Co., Texas, 12-VII-27, L. A. Stephenson (UKL).

Derivation of specific epithet: named after Karl Stephan, an accomplished amateur coleopterist who collected the holotype.

Notes on habitat: The type locality is in an area of desert grassland. I visited it, but failed to obtain specimens of this species.

Geographical relationships: The range partially overlaps that of *H. obliquus*, probably also that of *H. huachuca*, and possibly that of *H. cohni*. However, no instance of sympatry involving this species is known.

Geographical distribution: from western Texas to south-central Arizona (Fig. 13).

Harpalus (*Glanodes*) *obliquus* Horn

Harpalus obliquus Horn, 1889: 140. Type male, labelled as follows: "N.M.; LectoTYPE 2950 [red paper]; *H. obliquus* Horn" (ANSP). TYPE LOCALITY—Bayard, New Mexico (as indicated in original description).—Lindroth, 1968: 809.
Glanodes obliquus (Horn), Casey, 1914: 61.

Comparisons: The external characteristics of reduced elytral microsculpture and rounded humeri are sufficient to distinguish males of this species from other *Glanodes* males. The very narrow apical portion of the shaft, narrow apical disc, and large macrotrichial field F distinguish the male genitalia of this species from those of the closely related *H. cohni*.

Description: A specimen is illustrated in Fig. 12. Data on variation in standardized body length and in the ratios PL/EL, G: MWA/MLAP and G: ILV/ML are presented in Tables 1 to 4. Variation in the last 2 ratios is correlated in Graph 1. Elytra of males with microsculpture lines various: very fine, meshes broader than average, distinctly stretched transversely or lines of average depth and meshes approximately isodiametric; humeri not toothed (Fig. 3). Median lobe shorter than average, apical portion of shaft dorsally with numerous spinules throughout length, of average length; apical disc small, apex oblique, discal spinules well developed (Fig. 9a); apex narrow (Figs. 9b and 10). Internal sac with macrospine V slightly longer than average, macrotichial fields C and F large (Fig. 9a); 17 specimens were dissected.

Notes on habitat: I collected specimens on the San Augustin Plains of New Mexico, 40 miles from Magdalena at 7350′ above sea level, in grassland, adjacent to a wash which had recently been flooded. The soil was clay, reddish or gray in color, with stones on the surface. The beetles were found under cattle droppings and under stones where the soil was damp. Elsewhere the soil was very dry. Additional species represented there were: *Calosoma* (2 species); *Pasimachus californicus* Chaudoir; several species of *Bembidion*; *Agonum placidum* Say; 2 species of *Amara*; 8 harpalines, including *Piosoma setosum* LeConte, *Harpalus pensylvanicus* De Geer, *H. tadorcus* Ball, *H. amputatus* Say, a species of the *H. fraternus* group, 2 species of the *H. desertus* group, and 2 species of *Discoderus*; and 1 species of *Cymindis*. I did not see any especially distinctive features of the habitat, other than that the land was fairly well drained. It seemed to me that if *obliquus* specimens could live here, they could live anywhere on the San Augustin Plains.

Geographical relationships: The range includes that of *H. huachuca*, and probably, much of the range of *H. stephani*. However, it has yet to be established that *H. obliquus* populations are microsympatric with the populations of these other species.

Geographical distribution: known from western New Mexico and southeastern to south-central Arizona (Fig. 13).

Material examined: 35 specimens from the following localities:
ARIZONA: Cochise County: Chiricahua Mts., 14-IX-38 (OSUC); Hereford, 28-VII-07 (OSUC); Huachuca Mts. (AMNH, NMNH, OSUC); Webb (CAS). Graham County: Fort Grant (NMNH); Stockton Pass, Pinaleño Mts., 12-VIII-54 (UAT).
NEW MEXICO: Catron County: Rte. 78, 12.3 mi. nw. Beaverhead, 13-*IX*-67 7140′ (UASM); Rte. 78, 76 mi. sw. Magdalena, 17-VIII-69 (UASM). Grant County: Silver City, V. 13 (MCZ). Socorro County: "Socorro Co." (UKL); Magdalena, 18-VIII-94 (UKL); Magdalena Mts. VIII-94 (UKL); Rte. 78, 40.4 mi. sw. Magdalena, 7350′, 17-VIII-69 (UASM).

Harpalus (*Glanodes*) *cohni* Ball, NEW SPECIES

Comparisons: Males of this species are easily distinguished from other *Glanodes* males by the shining elytra whose intervals lack microsculpture. The elytra of *cohni* males are on the average relatively shorter; thus, the mean values for the ratio PL/EL are slightly higher than those of samples of other *Glanodes* males (see Table 2). The genitalia are markedly dis-

tinctive, with a reduced apical disc, large dorsal spinules, and elongate macrospine V (Fig. 11a and 11b). The mean differences between the population samples of this species and the Fraziers' Well sample of *H. puncticeps* are statistically significant, and the difference in the means of the ratio G: MWA/MLAP is taxonomically significant (Tables 3 and 4).

Description: Data on variation in standardized body length and in the ratios PL/EL, G: MWA/MLAP and G: ILV/ML are presented in Tables 1 to 4. Variation in the last 2 ratios is correlated in Graph 1. Elytra of males shining, with microsculpture lines very faint, confined to striae; humeri not toothed. Median lobe elongate; apical portion of shaft elongate, dorsally with longer than average spinules; apical disc oblique, small, without discal spinules (Fig. 11a); apex broad (Fig. 11b). Internal sac with macrospine V long; macrotrichial field C large, field F absent (Fig. 11a); 23 males were dissected.

Type material: HOLOTYPE male and ALLOTYPE female labelled: "Marfa, Texas, VII. 12, J. W. Green collector; J. W. Green collection" (CAS). PARATYPES: 36 males, 16 females, from the following TEXAS localities: Jeff Davis County: Fort Davis, 8-VI-14 (Fall Coll. MCZ); Davis Mts., s. slope, nr. Fort Davis, ca. 5000′, 8-VII-59 Ball family (UASM); Davis Mts., 9-VII, J. W. Green (CAS); same, 20-VIII-14 (Fall Coll., MCZ); same, 6-VII-07, Wenzel (OSUC); "Texas", Wenzel (Probably Davis Mts., OSUC). Presidio County: Marfa, 12-VII-11, J. W. Green (CAS, OSUC, FNMH); Marfa, 4600-4800′, 3-VII-06 Wickham (NMNH); 3 mi. nw. Marfa, 7-IX-51 T. J. Cohn (UASM).

Variation: The mean difference in standardized body length between the Davis Mountains and Marfa samples is slight but statistically significant (Table 1).

Derivation of the specific epithet: named in honor of the orthopterist Theodore J. Cohn, who, over the years, has contributed many fine beetles to my collection, including 1 of the paratypes listed above.

Notes on habitat: I found specimens at about daybreak on the lower slopes of the Davis Mountains in grassland. The soil was clay and sand and was very dry.

Geographical relationships and distribution: The range is not known to overlap the ranges of other *Glanodes* species, and it is at the southeasternmost edge of the area known to be occupied by the members of this subgenus (Fig. 13).

Species inquirendum

Glanodes regressus Casey, 1914: 62. HOLOTYPE female, labelled as follows: "Ari· [dot red]; Casey bequest 1925; TYPE USNM 47737 [red paper].—TYPE LOCALITY.—"near Benson" (from the original description).

This specimen is a female, though Casey declared the type to be a male; but he also wrote that the anterior tarsi were "nude beneath". He stated that the front tarsi of male *Glanodes* were unmodified, and this was the basis for including the group in his tribe Daptini. This specimen probably is a member of *H. obliquus* Horn, but because of its sex a certain identification cannot be made. Furthermore, the type locality is within or near the ranges of 3 species, and so an assignment based on geographical grounds cannot be made.

Specimens not identified

Females only were collected in the following localities, and so they could not be identified by association with sympatric males. Arizona: Cochise County: 11 mi. e. Sells (TLE); Texas Pass, Dragoon Mts. (CAS); Tucson (NMNH and UCB). New Mexico: Dona Ana County: 17 mi. ne. Las Cruces, Jornada Expt. Sta., 3-X-70 (TTUL); Eddy County: Malaga, 11-VII-36 (UKL).

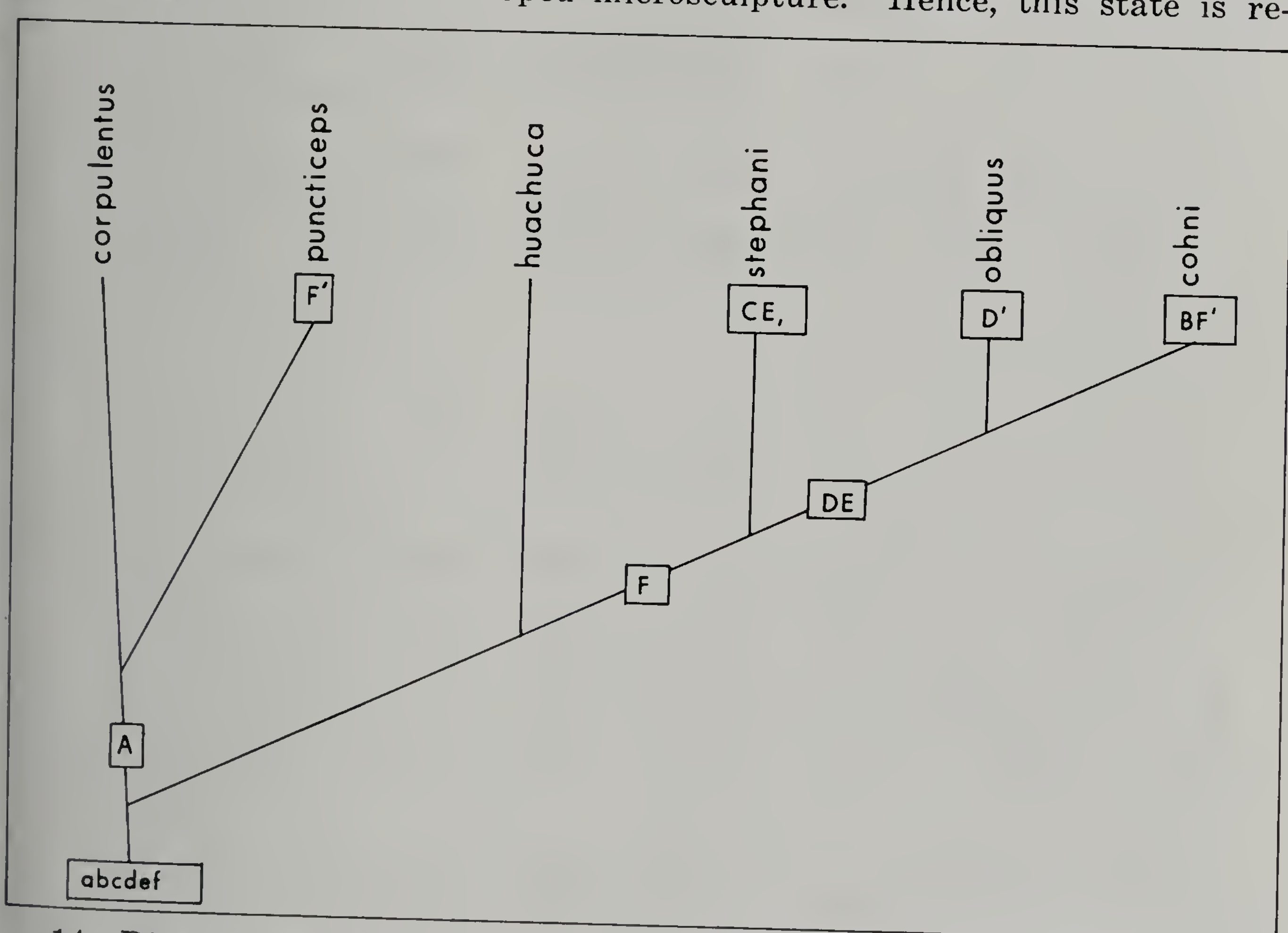
Phylogeny of the Species of *Glanodes*

My views on this topic are illustrated in Figure 14. This is a conventional time-divergence diagram, with time on the vertical axis and structural divergence on the horizontal axis. Each character state is designated by a letter: lower case for plesiotypic conditions and capitals for apotypic states (see Ball and Erwin, 1969).

Decisions about phylogenetic classification of character states were based either on frequency of occurrence within the subgenus, or on the development of transformation series or morphoclines. Species with an accumulation of plesiotypic characteristics were regarded as primitive and as representatives of earlier-evolved lineages; those with a majority of apotypic states were judged to be later in origin. Reasons for the assignment to category of each character state are presented below. A summary is presented in Table 5.

Elytral humeri: Because the common state in the Harpali as a whole is untoothed humeri, and because this state is the commonest one in *Glanodes*, it is regarded as plesiotypic.

Elytral microsculpture: The most common state in the Harpali as well as in *Glanodes* is well developed microsculpture. Hence, this state is re-



14. Diagram showing hypothetical phylogeny of the species of subgenus *Glanodes*. See Table 5 for explanation of letters.

garded as plesiotypic. I would also note some evidence of a morphocline in this characteristic. There is a tendency among *H. obliquus* males for marked reduction of microsculpture. This condition is intermediate between the conditions well developed and absent, and locates the *obliquus* line between the *cohni* line and the other *Glanodes* lines.

Median lobe, form: Of the 2 character states observed among *Glanodes* members, the curved condition is more widespread both in the Harpali and in *Glanodes*. Therefore, this state is judged to be plesiotypic.

Median lobe, apex: The broader apex is more widespread both in the Harpali as a whole, and in *Glanodes*. Therefore, it is judged to be the plesiotypic state.

Median lobe, dorso-apical spinules: There are 3 conditions: 1) present, small; 2) present large; 3) absent. The presence of spinules is regarded as plesiotypic relative to "spinuless" because the former is the more widespread in the subgenus. Both large spinules and no spinules are associated with generally more highly derived types of male genitalia, and so those states are regarded as apotypic.

Internal sac, macrospine V: This transformation series is based on the *a priori* assumption that the direction of evolution has been from a short spine to a long one, with intermediate conditions representing intermediate evolutionary stages. Also, the macrospines of *Harpalus* males of other groups tend, on the whole, to be shorter. Thus, the shortest macrospine

TABLE 1: DATA ON VARIATION IN STANDARDIZED BODY LENGTH (MM) AMONG MALES OF THE SUBGENUS GLANODES

SPECIES & LOCALITY	N	RANGE	x±SE	SD	CV%
corpulentus					
Wasatch, Utah	2	8.92 – 9.18	9.05		
Virgin River, Utah	1	9.00			
puncticeps					
Peach Springs, Arizona	2	9.68 – 10.22	9.95		
s. Frazier's Well, Arizona	12	8.75 – 10.25	9.48±0.15	0.49	5.16
nr. Paulden, Arizona	1	7.42			
huachuca					
Huachuca Mts., Arizona	1	8.85			
stephani					
Baboquivari Mts., Arizona	2	9.22 – 10.02	9.62		
Arivaca, Arizona	1	9.65			
Culberson Co., Texas	1	9.00			
obliquus					
Magdalena Mts., N. M.	2	8.65 – 9.10	8.88		
41 mi. sw. Magdalena, N. M.	3	8.78 – 8.88	8.82		
Silver City, N. M.	1	8.00			
Ft. Grant, Arizona	1	8.60			
Stockton Pass, Arizona	1	6.98			
Webb, Arizona	1	8.00			
Chiricahua Mts., Arizona	1	7.72			
Hereford, Arizona	1	8.78			
Huachuca Mts., Arizona	4	7.72 – 8.78	8.40		
cohni					
Davis Mts., Texas	9	8.10 – 8.32	8.81±0.14	0.39	4.46
Marfa, Texas	13	8.65 – 9.70	9.22±0.08	0.29	3.16

V of *Glanodes* males is the closest approach to the average condition of macrospine length in other groups of *Harpalus*.

The most primitive species is *H. huachuca*, its males exhibiting no apotypic character states. The most derivative species is *H. cohni*, whose males exhibit only 1 plesiotypic state. The other species occupy various intermediate positions.

The most discordant element in this scheme is *H. stephani*. The male genitalia do not fit in with those of the other taxa, except that in proportions the specimens of *H. stephani* are intermediate in position (see Graph 1). The only other assumption that one could make concerning the relationships of *H. stephani* is that it represents the sister group of all of the other species of the subgenus.

Another rather discordant element is the elongate macrospine V of *puncticeps* males. This is believed to be a highly derived characteristic, and it seems strange appearing in an otherwise rather primitive stock. The assumption required is that macrospine V became elongate twice.

This hypothetical phylogeny is discussed further, in terms of geographical distribution of the extant taxa.

Zoogeography of the Species of *Glanodes*

Only very general statements can be made about the possible geographical history of *Glanodes* because: 1) the sister group of the sub-

TABLE 2: Data on Variation in the Ratio PL/EL Among Males of the Subgenus Glanodes

Species & Locality	N	Range		x±SE	SD	CV%
corpulentus						
Wasatch, Utah	2	0.39 –	0.40	0.39		
Virgin River, Utah	1			0.39		
puncticeps						
Peach Springs, Arizona	2	0.40 –	0.42	0.41		
s. Frazier's Well, Arizona	12	0.40 –	0.45	0.42±0.004	0.014	3.34
nr. Paulden, Arizona	1	0.43				
huachuca						
Huachuca Mts., Arizona	1			0.41		
stephani						
Baboquivari Mts., Arizona	2	0.39 –	0.41	0.40		
Arivaca, Arizona	1	0.42				
Culberson Co., Texas	1	0.41				
obliquus						
Magdalena Mts., N. M.	2	0.38 –	0.40	0.39		
41 mi. sw. Magdalena, N. M.	3	0.40 –	0.41	0.40		
Silver City, N. M.	1	0.40				
Ft. Grant, Arizona	1	0.40				
Stockton Pass, Arizona	1	0.42	0.42			
Webb, Arizona	1	0.42				
Chiricahua Mts., Arizona	1					
Hereford, Arizona	1	0.43				
Huachuca Mts., Arizona	4	0.42 –	0.43	0.42		
cohni						
Davis Mts., Texas	9	0.42 –	0.46	0.44±0.005	0.014	3.26
Marfa, Texas	13	0.43 –	0.48	0.45±0.004	0.014	3.04

genus is unknown, so the area of origin is uncertain; 2) little is known about the actual geographical ranges of the extant taxa; 3) even less is known about the ecological requirements of these species. The history of the extant taxa is inferred from the probable history of the plant communities of which they are a part. It is likely that these taxa are confined to arid grasslands, and this is assumed to be true. It seems desirable to use the information available to make a preliminary assessment of the history and evolution of *Glanodes*.

The pattern: The ranges of 3 species overlap in Arizona, and 4 of the 6 known species occur in that state. Beyond southern Arizona, single species are encountered: to the north and west, *H. puncticeps* and *H. corpulentus*; to the northeast, *H. obliquus*; to the southeast, *H. cohni*. Southward, in Mexico, the group is not known to be represented. Probably this is the result of insufficient collecting.

These species are represented in grassland-type habitats, associated with the edges of deserts: *H. corpulentus* with the Great Basin desert; *H. puncticeps, H. huachuca, H. stephani,* and *H. obliquus* with the Sonoran desert; *H. obliquus, H. stephani,* and *H. cohni* with the Chihuahuan desert.

The grassland habitats are more or less discontinuous, occurring in the south along the flanks of mountain ranges at elevations of 3500 to 5000 feet (Lowe, 1964: 40). Farther north, above the Mogollon Rim, near the Grand Canyon in Arizona, isolated patches of grassland are at elevations between 5000 and 7000 feet. In New Mexico, the San Augustin Plains,

TABLE 3: Data on Variation in the Ratio G: MWA/MLAP Among Males of the Subgenus Glanodes

Species & Locality	N	Range	$\bar{x} \pm SE$	SD	CV%
corpulentus					
Wasatch, Utah	2	0.47	0.47		
Virgin River, Utah	1	0.53			
puncticeps					
Peach Springs, Arizona	2	0.42 – 0.47	0.44		
s. Frazier's Well, Arizona	12	0.36 – 0.53	0.44±0.01	0.05	10.78
nr. Paulden, Arizona	1	0.35			
huachuca					
Huachuca Mts., Arizona	1	0.47			
stephani					
Baboquivari Mts., Arizona	2	0.42 – 0.47	0.40		
Arivaca, Arizona	1	0.44			
Culberson Co., Texas	1	0.38			
obliquus					
Magdalena Mts., N. M.	2	0.22 – 0.26	0.24		
41 mi. sw. Magdalena, N. M.	3	0.21 – 0.25	0.23		
Silver City, N. M.	1	0.25			
Ft. Grant, Arizona	1	0.25			
Stockton Pass, Arizona	1	0.21			
Webb, Arizona	1	0.30			
Chiricahua Mts., Arizona	1	0.22			
Hereford, Arizona	1	0.23			
Huachuca Mts., Arizona	4	0.25 – 0.27	0.26		
cohni					
Davis Mts., Texas	9	0.26 – 0.33	0.30±0.01	0.02	6.48
Marfa, Texas	13	0.25 – 0.32	0.30±0.01	0.02	8.51

surrounded by woodland communities, support grassland. North of the Grand Canyon, the non-arboreal plant communities consist mainly of desert shrub and grasses (Hunt, 1956: Fig. 5). These areas are isolated from the more southerly portions of Arizona by the Colorado River valley, especially by the Grand Canyon, and by the barren Painted Desert and adjacent plateaus. In western Texas, grassland occurs along the slopes of the Davis Mountain—Guadalupe Mountains system (Martin and Mehringer, 1965: Fig. 3). The present fragmented distribution of these habi-

TABLE 4: DATA ON VARIATION IN THE RATIO G: ILV/ML AMONG MALES OF THE SUBGENUS GLANODES

SPECIES & LOCALITY	N	RANGE	$x \pm SE$	SD	CV%
corpulentus					
Wasatch, Utah	2	0.22	0.22		
Virgin River, Utah	1	0.22			
puncticeps					
Peach Springs, Arizona	2	0.31 – 0.33	0.32		
s. Frazier's Well, Arizona	12	0.32 – 0.36	0.33±0.004	0.014	4.13
nr. Paulden, Arizona	1	0.35			
huachuca					
Huachuca Mts., Arizona	1	0.20			
stephani					
Baboquivari Mts., Arizona	2	0.27 – 0.28	0.275		
Arivaca, Arizona	1	0.25			
Culberson Co., Texas	1	0.25			
obliquus					
Magdalena Mts., N. M.	2	0.29 – 0.31	0.30		
41 mi. sw. Magdalena, N. M.	3	0.25 – 0.31	0.28		
Silver City, N. M.	1	0.31			
Ft. Grant, Arizona	1	0.29			
Stockton Pass, Arizona	1	0.31			
Webb, Arizona	1	0.26			
Chiricahua Mts., Arizona	1	0.21			
Hereford, Arizona	1	0.25			
Huachuca Mts., Arizona	4	0.26 – 0.29	0.27		
cohni					
Davis Mts., Texas	9	0.35 – 0.39	0.37±0.004	0.012	3.32
Marfa, Texas	13	0.34 – 0.39	0.36±0.004	0.014	3.73

TABLE 5: PHYLOGENETIC CLASSIFICATION OF CHARACTER STATES OF *Glanodes* SPECIES.

CHARACTER	STATE			
	Plesiotypic		Apotypic	
Elytral humeri	not toothed	(a)	toothed	(A)
Elytral microsculpture	evident	(b)	not evident	(B)
Median lobe, form	curved	(c)	straight	(C)
Median lobe, apex	broad	(d)	narrow	(D)
			very narrow	(D′)
Median lobe, spinules	present, small	(e)	present, large	(E)
			absent	(E′)
Macrospine V	short	(f)	long	(F)
			longer	(F′)

tats no doubt accounts for the discontinuous ranges of the *Glanodes* taxa. The allopatry of the species suggests rather extended periods of isolation of these grassland areas. The range of *H. corpulentus* is isolated from the ranges of the other species by the canyon of the Colorado River.

During the Pleistocene, the ranges of the species of *Glanodes* must have been somewhat different from what they are today, for most of the southwestern grasslands were invaded by pine-parkland, at least during Wisconsin time (Martin and Mehringer, 1965: 439). Under these conditions, the ranges and dispersal potential of *Glanodes* populations probably were more limited than they are today. At other times, dispersal potential was probably enhanced by conditions favorable to expansion of grassland areas.

Present range discontinuity implies past continuity, and the explanation for this is likely to be in terms of past climatic events. Also to be accounted for is the relatively high concentration of *Glanodes* species in southern Arizona.

Finally, to be accounted for is a general relationship between the phylogenetic pattern and the distribution pattern of the species. The more primitive species are in the west and north; the more derivative ones are in the south and east.

Historical zoogeography: The present pattern is explained as follows. The ancestral stock of the extant species of *Glanodes* originated in the semiarid areas of the Colorado Plateau, probably north of the Grand Canyon, after the major deserts had developed (i.e. mid-Pliocene time; see Axelrod, 1948). Thus this stock was hemmed in by the Great Basin deserts to the west, by forests to the north, and by mountains to the east. Dispersal southward across the plateau was possible, if the Grand Canyon had not yet developed, and this seems likely (Hunt, 1956: Fig. 61). This early stock eventually spread to southern Arizona, survived in the grassland areas there and in the north, but died out in the country adjacent to the Mogollon Rim. This provided 2 isolated groups of *Glanodes*: a northwestern one and a southwestern one. The northwestern stock diverged in relation to the southwestern one, and later, differentiated to produce different species on opposite sides of the Grand Canyon. Implied here is that the route southward was interrupted before the Grand Canyon was deep enough to form a virtually impassable barrier to dispersal of flightless insects.

In the south, the range of the original invading stock became fragmented; differentiation took place, to produce *H. huachuca* and the ancestor of the *H. stephani-obliquus-cohni* lineage. During a climatically favorable interval, the latter stock became more widespread, ultimately giving rise to *H. stephani* in Arizona, *H. obliquus* in New Mexico, and *H. cohni* in Texas. This likely involved one or more cycles of range contraction-isolation-differentiation followed by dispersal. During a relatively recent favorable period, *H. obliquus* dispersed westward to enter Arizona and *H. stephani* moved eastward into New Mexico and Texas. Finally the ranges of *H. stephani* and *H. obliquus* became interrupted by recurrence of unfavorable conditions.

Most of these alternating episodes of dispersal and isolation-differentiation must be related to events of Pleistocene time, even though it seems

that this span is not sufficiently great to permit this amount of speciation. For example, evidence derived from more northern fossil carabids does not suggest that differentiation has taken place during the Pleistocene (Coope, 1970: 106). Further, Hopkins, *et al* (1971) show that differentiation of some carabids likely took place between late Pliocene and the present. I suggest that if these *Glanodes* taxa were older one might reasonably expect wider geographical ranges, more instances of sympatry, and additional species in other, more remote geographical areas. I believe, therefore, that the rate of differentiation of this group was more rapid than average.

It is known that grassland areas were invaded by woodlands during the Wisconsin glacial stage. In the more xeric post-glacial times, the woodland withdrew to more mesic situations, and desert and grassland were able to expand. Fire may have been a factor in the restriction of woodland (Humphrey, 1956; Wells, 1970). Of course, as areas become more xeric, grasslands are replaced by deserts. Possibly then, the desert grasslands were at their maxima for brief periods following termination of pluvial intervals, and during such periods, dispersal of *Glanodes* may have taken place. Conversely, fragmentation of the grasslands probably occurred both during dry and wet periods.

The above interpretation accounts for the general phyletic pattern of *Glanodes*, but it does not explain why there are more species in southern Arizona than elsewhere. I think this is the result of the presence of desert mountains in southern Arizona, the bases of which probably provided favorable sites for isolated grassland refugia during periods of excessive drought. These refugia would have permitted the initial differentiation of the *Glanodes* lineage in the south and the survival of the early descendants, *H. huachuca* and *H. stephani*. These stocks were joined later by *H. obliquus* populations.

This highly speculative account of the dispersal and evolution of *Glanodes* may be substantially modified when more is known about relationships of the subgenus and about the distribution and ecological requirements of the extant species. This small group would seem ideal for a detailed study of comparative ecology and speciation, and the additional information obtained would provide the evidence for evaluating the hypotheses presented above. Such work could best be done by a person living in southwestern United States.

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BOOK REVIEW

The compleat naturalist; a life of Linnaeus by Wilfrid Blunt. 1971. The Viking Press, Inc., 625 Madison Ave., N.Y., N.Y. 10022. 256 p.; numerous illustrations; $14.95, cloth. (With an appendix on Linnaean classification, nomenclature, and method by William T. Stern, p. 242-252).

No botanist or zoologist can ever be quite as famous and universally known as Linnaeus (or often just L.—even John F. Kennedy needs 3 letters [JFK]) for recognition. Only Fabricius (lesser known because of his narrower specialization) is easily recognized, at least by Coleopterists, by one initial (F.). Linneaus not only founded our present binomial system of nomenclature (1758), but he described approximately 4,400 species of animals and 7,700 species of plants.

The Linnaean Society of London has had most of Linnaeus' insect collections since 1829, but some are also deposited at the Zoological Institute in Uppsala, Sweden. Although several books, and many articles, have dealt with the life of Linnaeus, none is more beautifully executed than this new one. Although the emphasis is on his botanical activities, much of the text relates to the man and his ideas. It would be profitable reading for every biologist—but a must for every serious student of Coleoptera.—R. E. Woodruff.